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BIOLOGY OF HYDRACTINIID HYDROIDS. 4. ULTRASTRUCTURE OF THE PLANULA OF *HYDRACTINIA ECHINATA*

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ABSTRACT

The fine structure of the ectodermal surface of the planula larva of *Hydractinia echinata* is described and the spatial distribution of cell types quantified. The larval ectoderm contains five cell types: nematocytes, gland cells, epitheliomuscular cells, neurosensory cells, and nerve cells. Nematocytes (atrichous isorhizas and desmonemes) and neurosensory cells are clustered at the tapered posterior end of the larvae. Mucous cells occur over the surface of the planula, but are particularly common at the anterior end. The larva is similar to others described from marine hydroids, except that (a) gland cells display a ring of microvilli emerging from a cavity encircling the cilium and (b) nerve cells appear to lack a cilium.

INTRODUCTION

A number of sessile marine invertebrates settle preferentially in locations which are buffered from certain physical and biotic stresses (Meadows and Campbell, 1972; Scheltema, 1974; Buss, 1979). Certain sessile species are found in symbiosis with mobile organisms: such associations act to simultaneously limit access of predators and competitors which are unable to locate these surfaces (Jackson, 1977). Among the most specific of these relationships is the symbiosis of sessile species with hermit crabs of the genus *Pagarus* in coastal waters and scallops of the genus *Acopecten* in deeper waters. The relatively low diversity of sessile species occupying these habitats and the apparent specialization of various hydroid (*e.g., Hydractinia* and *Podocoryne* spp.), bryozoan (*e.g., Alcyonidium* spp.), and gastropod (*e.g., Crepidula* spp.) species on them, suggests that specialized mechanisms have developed which allow the location of these refugia and the discrimination of these substrata from others.

Hydractinia echinata is found primarily on hermit crab shells, although anecdotal accounts of *H. echinata* on other substrata are known (*e.g., Limulus* and other crab carapaces, pilings, and rock substrata). Planulae are capable of sensing movement of nearby objects and are reported to discharge nematocysts to latch onto passing substrata (Chia and Bickell, 1978). Studies of microfloral induction of metamorphosis have demonstrated that certain bacterial species release a metabolite which initiates *Hydractinia* settlement, an effect which can be mimicked by certain monovalent cations (Muller, 1969, 1973; Spindler and Muller, 1972). These same gram-negative bacterial species are found in association with hermit crabs (Muller, 1969).

While the planulae of Anthozoa, Hydrozoa, and to a lesser extent Scyphozoa display considerable cellular differentiation of the ectoderm (see review by Chia and Bickell, 1978), the relationship between planula behavior and planula fine structure is incompletely known. In several species, gland cells appear in the planulae which

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are not expressed in the adult, suggesting that glandular secretions play a functional role in attachment (Chia and Crawford, 1977; Vandermeulen, 1974; Martin and Thomas, 1977; Martin *et al.*, 1983). In addition, several planulae possess specialized ciliary structures, putatively sensory in function, which are postulated to play a role in habitat choice (Lyons, 1973; Vandermeulen, 1974; Mariscal, 1974a; Martin and Thomas, 1977; Chia and Koss, 1979; Martin *et al.*, 1983). Nerves and neurosensory cells are present in most species studied and are known, in some species, to play an important role in settlement (Martin and Thomas, 1977, 1981a, b; 1983). Although the fine structure of several planulae have been described, the planulae of *Hydractinia*, whose behavior is well known, have no such description. As a prelude to experimental analysis of structure—function relationships in *H. echinata* planulae, we describe the ultrastructure of competent planulae, with emphasis on the nature of ectodermal cells.

MATERIALS AND METHODS

Hydractinia echinata is a dioecious hydroid, whose spawning is initiated in response to light (Bunting, 1894; Ballard, 1942). Laboratory cultivated colonies (Ivker, 1972) were placed in aerated dishes overnight and fertilized eggs were collected the following morning. Fertilized eggs develop into competent planulae within 18 h at room temperature. Planulae used for ultrastructural observations varied in age from 24 to 96 h post-fertilization. Planulae were fixed for 2 h at room temperature in 4% glutaraldehyde in 0.1 *M* sodium cacodylate buffered, double-strength, filtered sea water at pH 7.0. Planulae were rinsed in buffer for three successive 10 minute washes and then post-fixed in 2% OsO_4 in 0.1 *M* sodium cacodylate in distilled water at pH 7.0 for 1 h at room temperature. After a second series of three ten-minute washes in buffered sea water, specimens for transmission electron microscopy (TEM) were then infiltrated with propylene oxide and embedded with a Spurr's epoxy mixture of 70°C overnight. Blocks were sectioned on a Huxley ultramicrotome, stained with uranyl acetate and Reynold's lead citrate, and viewed with a Philips 300 series transmission electron microscope. Sections ranged in thickness from 700–2200 Å (silver to blue). Thick sections (purple and blue) were made in order to frequently capture the cilia of the mucous cell and relatively rare neurosensory cell. Specimens for scanning electron microscopy (SEM) were fixed as described above, dehydrated in an ethanol solvent, critical point dried in a Balser critical point dryer with CO_2, mounted on stubs, sputter coated with paladium and gold, and viewed with an ISI-40 scanning electron microscope. Several hundred sections were observed and complete serial sections made for gland, epitheliomuscular, and nerve cells. The relative frequency of epitheliomuscular cells, nematocytes, sensory, and mucous cells was quantified from scanning electron micrographs. At each of four locations on the surface of the planula, the number of each cell type present was counted for a total of ten planulae. For each planula, the total area sampled per location was chosen so that the number of each cell type per unit area was constant.

RESULTS

The planula of *Hydractinia echinata* is cone-shaped, 300–500 μm long and 100–120 μm wide, with a blunt anterior end and a tapered posterior tip. At the blunt end, the planula contains a distinct dimple (Fig. 1). The planula is uniformly ciliated, with ciliary structures extending from each ectodermal cell. The ectodermal surface of the planula harbors five cell types: nematocytes, epitheliomuscular cells

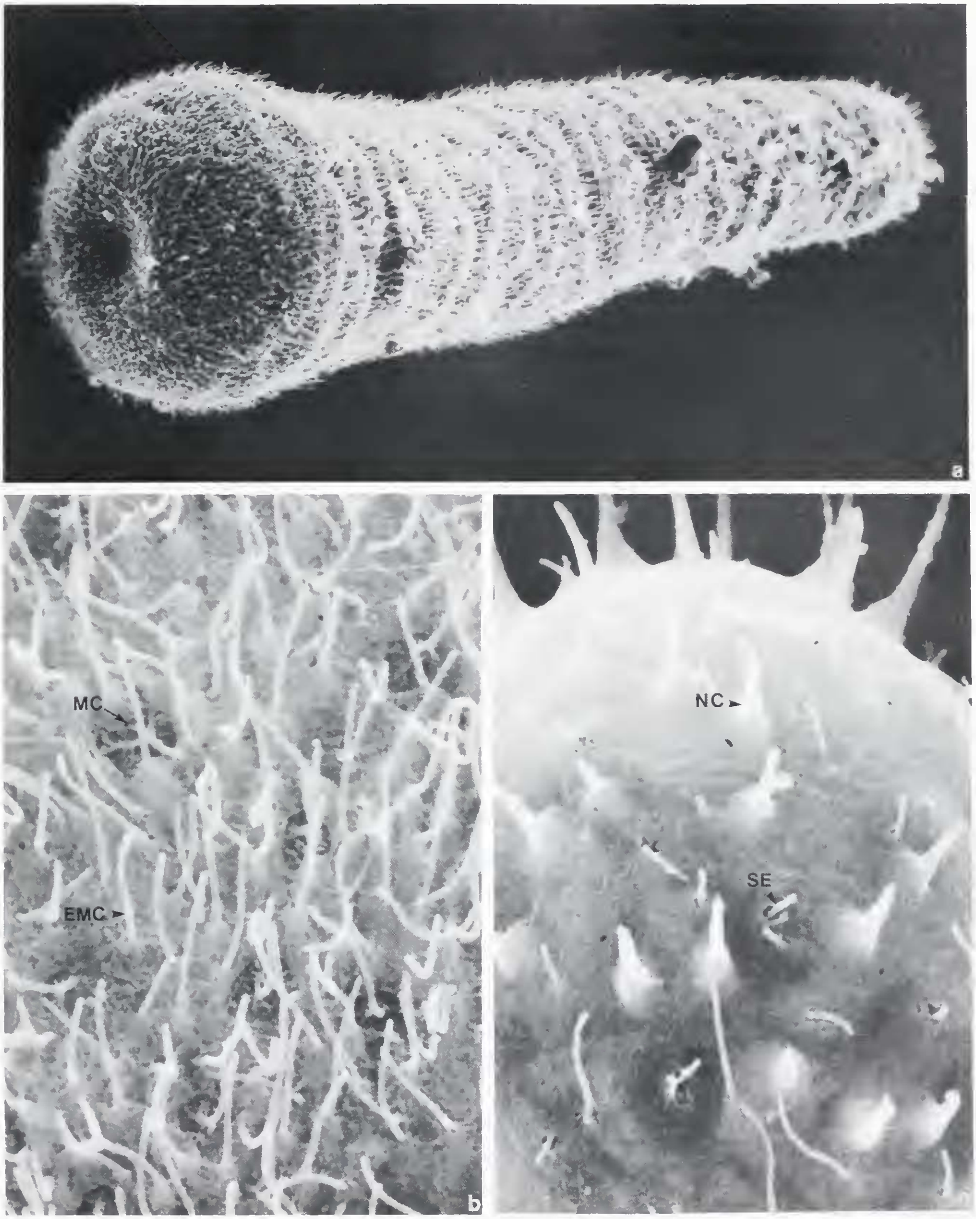

FIGURE 1. *H. echinata* planula. (A) Low magnification scanning micrograph of a planula (232×). (B) Scanning micrograph of the surface of a planula near the blunt end. Note uniform ciliation (2240×). (C) Scanning micrograph of the surface at the tapered tip (2240×). EMC = cilium of an EMC, NC = cnidocil emerging from a nematocyte, MC = cilium and associated microvilli emerging from a mucous cell, SE = cilium emerging from a concavity in a neurosensory cell.

(hereafter EMC), gland cells, neurosensory cells, and nerve cells. No interstitial cells were found in the ectoderm. The fine structure and relative frequency of each cell type is described below.

Nematocyte

Nematocytes (Figs. 3, 4) occur along the entire length of the planula, but are exceedingly dense at the tapered end (Fig. 2). Two types of nematocysts occur in the planula: atrichous isorhizas (Fig. 4A) and desmonemes (Fig. 4B) (*sensu* Mariscal, 1974b). The cnidoblast originates from interstitial cells in the endoderm. The external tube extends through the cytoplasm in the early stages of development, but invaginates completely before the cell's migration to the ectoderm. The cnidocil and its associated rods and stereocilia develop while the cell moves through the endoderm and ectoderm (Fig. 4C). At this stage, the nucleus is positioned under the basal end of the mature capsule (Fig. 4C). Mitochrondria with well developed cristae are prominent. Slightly to the side of the operculum are two centrioles

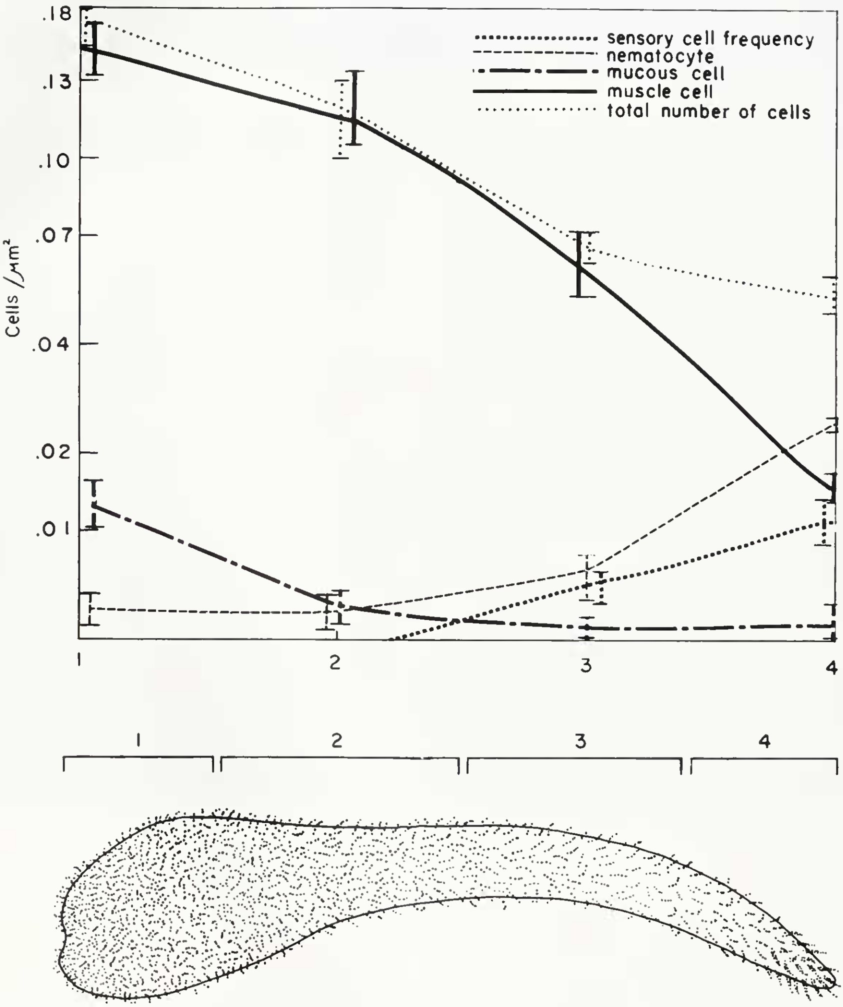

FIGURE. 2. Frequency of ectodermal cell types. Numerals refer to location on the surface of the planula as indicated.

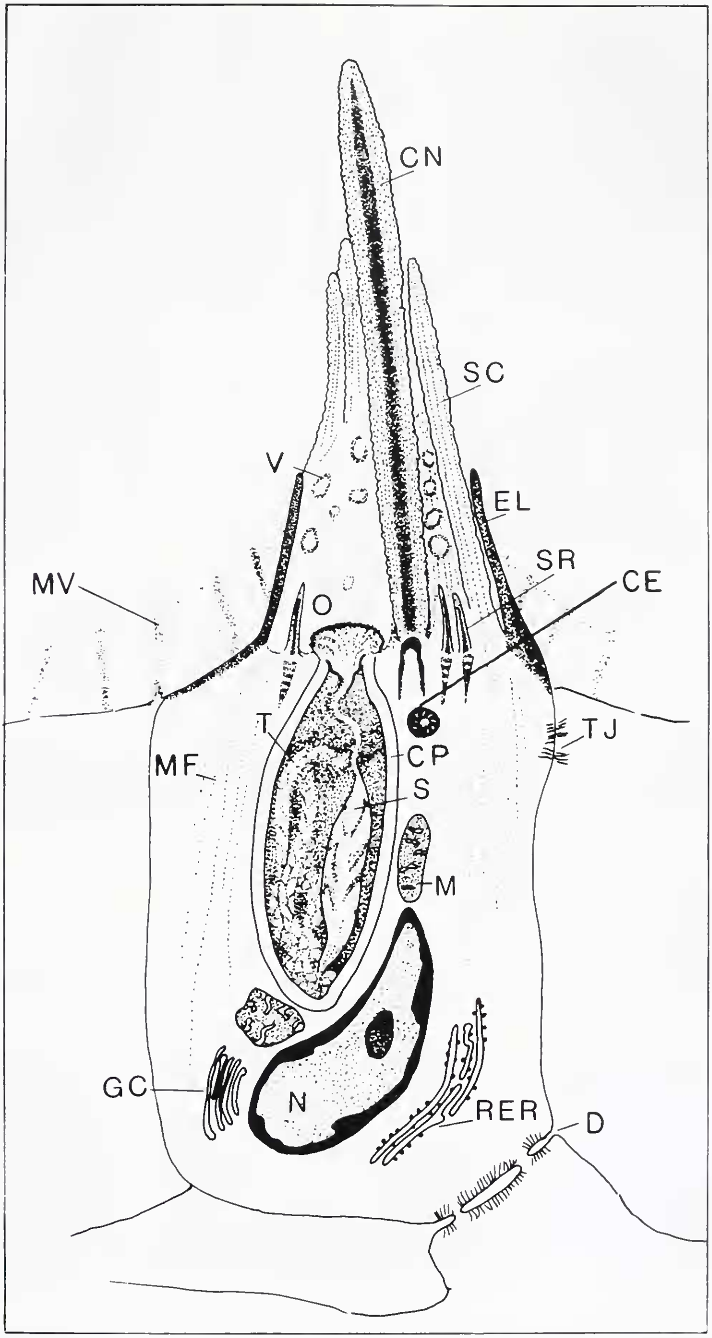

FIGURE. 3. Longitudinal reconstruction of the nematocyte extending outer ectodermal surface to the mesoglea. CE = centriole, CP = capsule, CN = cnidocil, D = desmosome, EL = epithelial lip, GC = Golgi Complex, M = mitochrondrion, MF = microfilaments, MV = microvillus, N = nucleus, O = operculum, RER = rough endoplasmic reticulum, S = stylet, SC = stereocilla, SR = stiff rod, T = thread, TJ = tight junction, V = irregularly shaped vesicles.

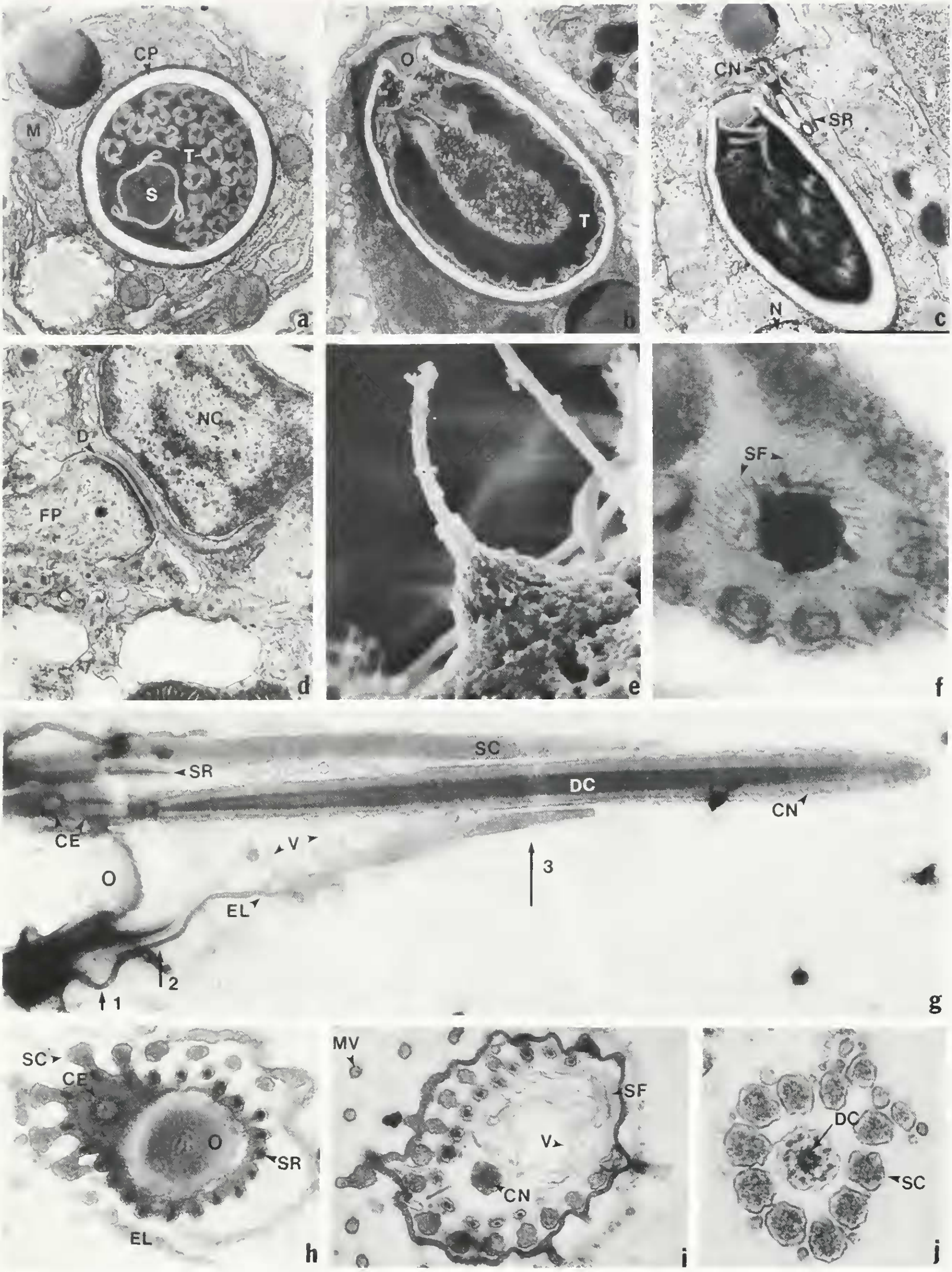

FIGURE 4. Nematocyte. (A) Cross-section of an atrichous isorhiza. Note the stylet and small thread (16,620×). (B) Longitudinal section of a desmoneme. Note the single large thread (16,620×). (C) Cnidoblast in the endoderm (10,234×). (D) Desmosome between the base of a nematocyte and a foot process of an EMC (16,620×). (E) A scanning micrograph of a cnidocil on the surface of a planula (8,867×). (F) Cross-section of a cnidocil and cnidocil-associated apparatus. Note the fine filamentous sheath can be seen surrounding the cnidocil and stereocilia (61,344×). (G) Longitudinal section of a cnidocil, cnidocil-associated apparatus, and operculum (16,080×). (H) Cross-section of centriole, cnidocil, and cnidocil-associated apparatus, and operculum of position of arrow #1 in (G) (28,080×). (I) Cross-

oriented at a 90° angle to each other, above which arises the partially formed cnidocil (Fig. 4C). The striated rootlet of a stiff rod lies to the right of the centrioles.

The mature nematocyte, 5–7 μm in length, extends from the ectodermal surface to the neuro-muscular layer except at the extreme posterior and anterior ends of the planula. Here the cell appears to be embedded in EMC's. A desmosome, 0.5 μm across, lies between the nematocyte and the foot process of an EMC near the base of the cell (Fig. 4D). The capsule of atrichous isorhizas, 1.5 μm in diameter and 4.5 μm in length, is composed of a dark-staining outer wall surrounding a light inner wall and houses the projectile apparatus of thread and stylet (Figs. 4A, C). The projectile apparatus of the desmoneme lacks a stylet, but contains a thickened thread (Fig. 4B). An operculum, 0.63 μm in diameter, caps the nematocyst (Figs. 4B, C, G). A large nucleus, approximately 3 μm long, is wrapped around the base of the capsule (Fig. 4C). The cytoplasm of the nematocyte contains rough endoplasmic reticulum (RER) (Fig. 4C), mitochondria, a dense stream of microfilaments, and a Golgi Complex (not shown in section) located near the nucleus.

The cnidocil (Figs. 4E, G–J), a modified cilium, 6.5 μm long and 0.27 μm in diameter, is characterized by nine doublets of microtubules around the edge of a dark staining inner core, 90 nm in diameter, apparently composed of many unpaired microtubules embedded in a dense unpackaged filamentous material (Figs. 4G, J). The inner core narrows at the top as the cnidocil tapers to a tip (Fig. 4G). Two centrioles comprise the base of the cnidocil (Figs. 4C, G). Twenty to twenty-four short, stiff rods, 0.62 μm long and 70–90 nm in diameter, with striated rootlets, 0.45 μm long, surround the base of the cnidocil and operculum (Figs. 4C, G–I). The striated rootlets closely resemble those of cilia of the EMC. The stiff rods are partially surrounded by 9–14 stereocilia (Figs. 4H, I), 3.8–4.7 μm long and 90–140 nm in diameter, containing a dense array of microfilaments (Figs. 4H–J) that extend down to anchor in the cytoplasm. These large and long spatula-shaped projections encircle the cnidocil above the point where the stiff rods end (Fig. 4J). Also present in the cnidocil-associated apparatus are numerous thin-membraned, irregularly shaped vesicles of unknown content and function, ranging from 40–130 nm in diameter. These may be lined up between a stereocilium and the cnidocil (Fig. 4G) or may be scattered throughout the space above the operculum (Fig. 4I). The rods, stereocilia, and cnidocil are connected by, and embedded in, a matrix of fine filamentous sheets, spread approximately 30 nm apart (Fig. 4F).

Gland cell

The gland (or mucous) cell (Figs. 5, 6) is characterized by large, tightly packed, electron-lucent granules, a dense staining basal nucleus, one or more large dark staining bodies at the base, and a single short cilium with a short striated rootlet and associated centrioles. Gland cells are particularly large (30 μm long) and common at the dimpled end of the planula (Fig. 5A) and are less common along the edges and at the tip of the planula (6.6 μm long) (Fig. 5D), largely because the ectoderm itself narrows in this region (Fig. 2). The cilium is located in a depression, 1.2–1.7 μm in diameter, 1.8–2.4 μm deep, and 4.0–5.3 μm in circumference, and

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section of cnidocil and associated apparatus at position of arrow #2 in (G) (22,133×). (J) Cross-section of cnidocil and stereocilia at position of arrow #3 in (G). The nine doublets and dense inner core can clearly be seen as can the very fine array of microfilaments in the stereocilia (32,947×). DC = dense inner core, FP = foot process of EMC, NC = nematocyte, SF = sheet of fine filaments. Other labels as described in previous figures.

FIGURE 5. Gland cell. (A) Longitudinal section through the ectoderm of a planula at the blunt end (4462×). (B) Scanning micrograph of the cilium of a mucous cell on the surface of a planula. Note the basket of microvilli surrounding cilium, emerging from a concavity (17,113×). (C) Longitudinal section of a cilium and associated microvilli extending from depression in a mucous cell. Microvilli appear to emerge in groups from within crevices between mucous granules in the cytoplasm (11,198×). (D) Longitudinal section of two mucous cells near the tapered tip. Note that the concavities are rich in microvilli, that there is a large dense staining body at the base of one cell, and that both cells lie above a thin nerve layer and mesoglea (3631×). (E) A higher magnification of the basal ectoderm in (A). The mucous cells appear to be in close association with axons of nerve cells, both with and without neurosecretory granules. Microtubular foot processes of EMC's can also be seen extending down to the

is surrounded by a complex basket of elongated microvilli (Figs. 5B, C). This ring of microvilli extends well beyond the opening of the concavity and appears to emerge from between individual mucous granules (Figs. 5C). The light-staining mucoprotein granules, 0.7–1.3 μm in diameter, are wrapped in a thin matrix of cytoplasm and fill the entire cell, except for a region at the base of the cell containing RER, several mitochondria, and dark-staining bodies (0.8–1.4 μm in diameter) (Figs. 5A, G). The large, dark-staining, basal nucleus, 2.3–3.0 μm long, is found in close association with various neurosecretory granules and microtubular extensions of the nerve layer (Figs. 5A, E).

Epitheliomuscular cell

Epitheliomuscular cells (Fig. 5), the most common cells of the ectoderm (Fig. 2), are characterized by large membrane-bound, dense staining granules, a large medially located nucleus, a Golgi complex, numerous large mitochondria, and a single cilium with a 9 + 2 arrangement of microtubules, striated rootlet, and centrioles. The dense granules are concentrated in the apical cytoplasm. These may, however, vary considerably in size (mean: 0.6 μm, range: 0.18–0.75 μm in diameter), number (range: 15–48), and location. Large dark-staining bodies, often containing large white crystals, are occasionally found located near the nuclei of EMC's. Muscular feet at the base of the cell, rich in microtubules, spread out and interdigitate with nematocytes, nerve cells, and other EMC's (Fig. 5F). The cilia of EMC's are either in a concavity, approximately 0.7–1.0 μm in diameter and 1.5 μm deep, surrounded by a collar of cytoplasm or found emerging from a flat or slightly raised cell surface (Fig. 5F). Cilia in concavities are most common at the blunt end of the planula, whereas the flat or raised form is found distributed over the rest of the surface. No other morphological differences have been observed in EMC's displaying the two arrangements of cilia.

Neurosensory cell

The sensory cell (Fig. 7) is the rarest cell type in the ectoderm, reaching its highest concentrations of the posterior (tapered) tip. The cell is characterized by an abundance of dense-cored neurosecretory vesicles approximately 70–100 nm in diameter, one or more prominent Golgi Complexes, a medially located nucleus, and a short cilium that emerges from a concavity in the cytoplasm (Figs. 7A, B). Neurosecretory vesicles are typically concentrated at the base of the cell (Fig. 7C). The cilium lacks any associated microvilli. Some ciliary rootlets are extremely long, extending in one case 9.8 μm from the ectodermal surface to the top of the nucleus. The neurosensory cells at the tapered tip contain large dark-staining granules, approximately 0.2–0.45 μm in diameter, in the aboral cytoplasm (Fig. 7B). Sensory cells along the lateral surfaces of the planula lack these granules and contain an electron-lucent cytoplasm (Fig. 7C). No other morphological distinctions have been observed between neurosensory cells with and without dark-staining granules.

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basal ectoderm (5348×). (F) Longitudinal section of an EMC along the lateral edge of the planula. Note that the cilium emerges from a slightly raised surface (6405×). C = cilium, DB = dark staining body, EN = endoderm, MC = mucous cell, ME = mesoglea, NE = nucleus of EMC, NF = nerve and foot process layer, NG = neurosecretory granules, NM = nucleus of mucous cell. Other labels as in previous figures.

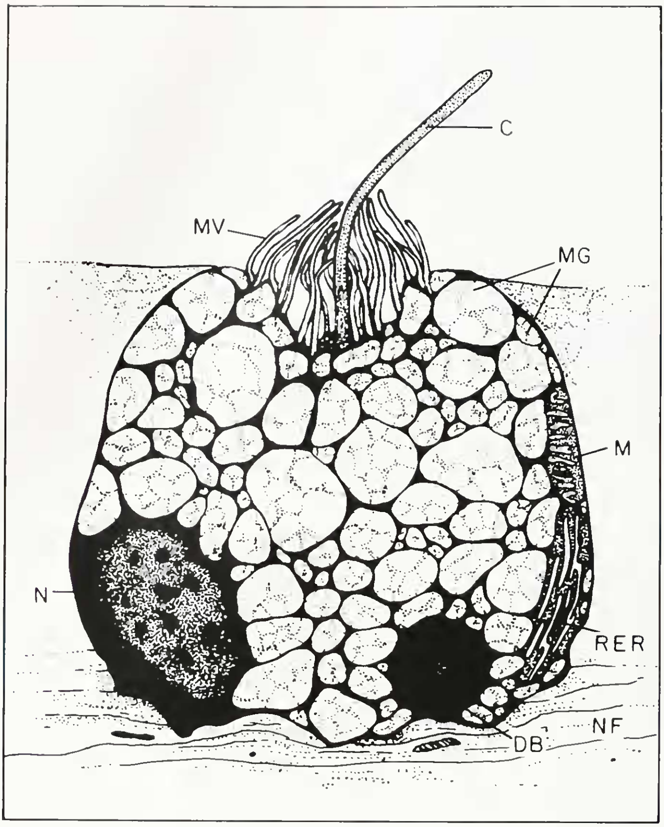

FIGURE 6. Longitudinal reconstruction of mucous cell extending from the outer ectodermal layer to the nerve layer. The mitochondrion and RER are characteristically located at the outer edge of the cytoplasm. MG = mucous granule. Other labels as in previous figures.

Nerve cell

The nerve layer ranges in thickness from 1 μm on the side of the planula to 6 μm at the blunt end, where numerous EMC's and mucous cells are found. The nerve cell (Figs. 7, 8) is the only cell type in the ectoderm, besides the cnidoblast, that is oriented parallel to the mesoglea. The cell is characterized by an irregularly shaped nucleus surrounded by perikaryon with neurites extending along the mesoglea 0.3–0.5 μm wide (Fig. 7D). A prominent Golgi Complex lies above the nucleus. Mitochondria vary in shape, from round in the perikaryon to extremely long in the neurites (Fig. 7D). Some neurites contain neurosecretory granules, approximately 70–100 nm in diameter, while others have only microtubules. It is not clear as to whether these different kinds of neurites occur in a single cell or whether they are derived from different cells. The dense inner core of the vesicles, found in both sensory and nerve cells, vary in both size and shape. Some have thin rectangular inner cores which are distinctly detached from their surrounding membrane, while others are entirely dense with no space between the membrane and the contents. Still others appear to have little or no contents. It is unknown whether this variation represents an artifact of fixation or significant differences in morphology, function,

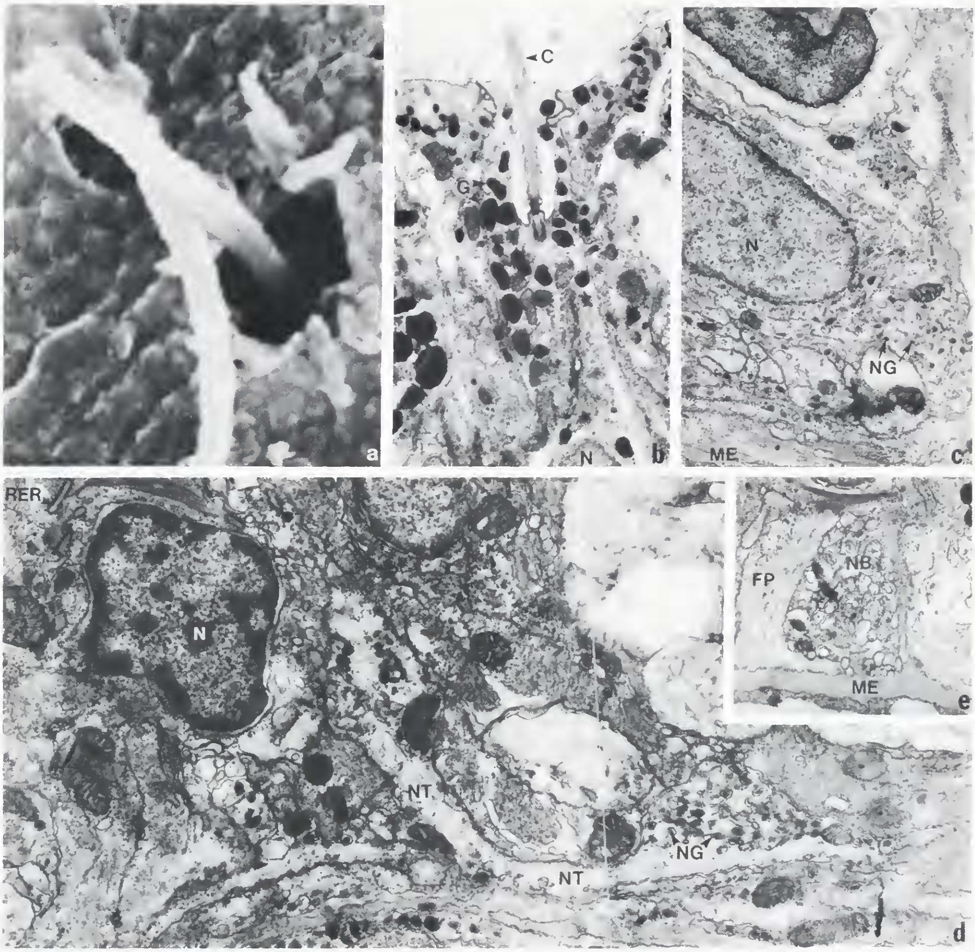

FIGURE 7. Sensory and nerve cells. (A) A scanning micrograph of a sensory cilium. Note its short length and that it emerges from a concavity (15,600×). (B) Longitudinal section of the apical end of a sensory cell at the tapered tip. Note the dark-staining granules in the apical cytoplasm (9521×). (C) Longitudinal section of the basal end of a sensory cell. The basal cytoplasm is rich in neurosecretory granules and can be seen interdigitating with neurites (9071×). (D) A nerve cell in the basal ectoderm. A neurite containing microtubules and neurosecretory granules extends into the nerve layer (15,350×). (E) Low magnification of a nerve bundle in cross-section in the basal ectoderm. The nerve bundle is surrounded by microtubular foot processes of EMC's (9720×). G = dark-staining granules, NB = nerve bundle, NT = neurite. Other labels as in previous figures.

or development. Neurites, often found packaged in large bundles (Fig. 7E), were observed in both longitudinal and cross-sectional sections. No cilium was found in serial sections of nerve cells.

DISCUSSION

While the ectoderm of the *Hydractinia echinata* planula possesses cells similar to those described for other cnidarian planulae, each cell type in *H. echinata* differs subtly from related cells in other species. A summary of the ectodermal cell types

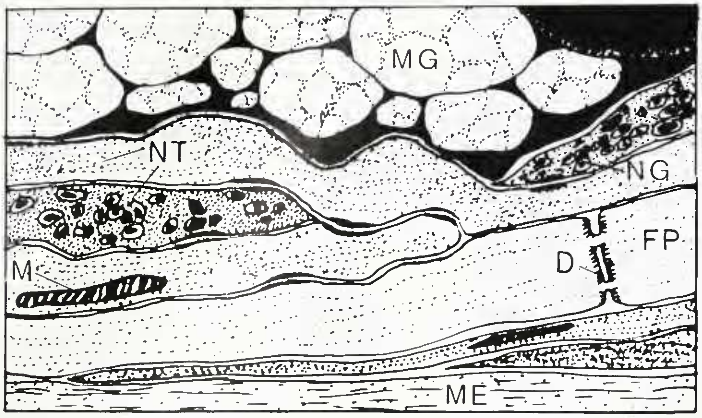

FIGURE 8. Reconstruction of nerve layer below a mucous cell. Neurites extend in both directions. Some contain microtubules, while others contain neurosecretory granules. Labels as in previous figures.

in cnidarian planulae, modified from Martin and Thomas (1977), is presented in Table I. Nematocytes, not studied in depth in many planulae, appear to have the same general cell structure as those described in adult hydroids (*e.g.*, Chapman and Tilney, 1959; Slautterback and Fawcett, 1959; Lentz, 1966, and many others), but with different nematocysts. The supportive cell or EMC of *H. echinata* very closely resembles that of the hydroids *Pennaria tiarella* (Martin and Thomas, 1977) and *Mitrocomella polydiademata* (Martin *et al.*, 1983) in both cell structure and content. All three extend from the mesoglea to the ectoderm and contain locomotory cilia. The EMC's of *P. tiarella* planulae, as in *H. echinata*, contain dense, membrane-bound granules at their apex, whereas *M. polydiademata* lacks apical granules and possesses large basal ones. *Mitrocomella polydiademata*, however, does possess a cell containing dense staining granules which may also be a supportive cell. In contrast to these hydroids, the supportive cells of the four described anthozoan planulae all lack dark-staining granules. The cilia of supportive cells in *Balanophyllia regia* (Lyons, 1973), *Pocillopora damicornis* (Vandermeulen, 1974), and *Anthopleura elegantissima* (Chia and Koss, 1979) all contain collar cells consisting of an ordered, symmetrical arrangement of microvilli around the cilium and complex bands of microfilaments associated with the striated rootlet of the cilium. No such apparatus is found in *H. echinata* or other described hydroid planulae.

The mucous cell of *H. echinata* is also very similar to mucous cells found in *P. tiarella* and *M. polydiademata*, except that these hydroids lack the concavity for the cilium and the associated microvilli found in *H. echinata*. All four anthozoan species possess several gland cells, including an electron-lucent mucous cell. Those of *Ptilosarcus gurneyi* and *P. damicornis* lack cilia and microvilli, but contain granules similar in size and concentration to those of *H. echinata*. The four different gland cells of the anthozoan *B. regia* are ciliated and possess "randomly arrayed microvilli" (Lyons, 1973), but the microvilli do not appear to be arranged in as ordered a fashion as those in *H. echinata*.

The sensory cell of *H. echinata* planulae lacking apical granules has counterparts in the hydroids *M. polydiademata* and *P. tiarella*. Comparable sensory cells occur in only one of the four anthozoan species. Chia and Koss (1979) describe two sensory cells in the ectoderm of the anemone *A. elegantissima* that resemble the sensory cell in *H. echinata*. Of the two cells, one possesses an electron lucent

TABLE I

*Distribution of ectodermal cell types**

Taxa	Reference	Number of ectodermal cell types							
		Total # cell types	Nemato-cysts	Supportive cells	Gland cells	Sensory cells	Nerve cells	Other cells	Uniformly ciliated
ANTHOZOA									
Anthopleura elegantissima	Chia and Koss, 1979, 1983	11	3	1	3	2	1	1	yes
Ptilosarcus gurneyi	Chia and Crawford, 1977	7	1	2	3	0	1	0	yes
Balanophyllia regia	Lyons, 1983	9	3	1	4	0	1	0	yes
Pocillopora damicornis	Vandermeulen, 1974	10	3	2	4	0	1	0	yes
HYDROZOA									
Mitrocomella polydiademata	Martin, 1983	6	1	1	2	1	1	0	yes
Pennaria tiarella	Martin and Thomas, 1977, 1981a,b, 1983	5	1	1	1	1	1	0	yes
Hydractinia echinata	This study	6	2	1	1	1	1	0	yes
SCYPHOZOA									
Haliclystus salpinx	Otto, 1978	3	1	1	0	0	0	1	no
Cassiopeia xamachana	Martin and Chia, 1982	2	1	1	0	0	0	0	yes

* Modified from Martin and Thomas, 1977.

cytoplasm without vesicles and the other contains large dense vesicles in the basal portion of the cell. These cells, however, are concentrated at the aboral end of the planula and are associated with the apical organ. The apical organ, with its associated cells and cilia, is far more sophisticated than any sensory structure in *H. echinata*. Nerve cells of *H. echinata* planulae closely resemble the sensory-motor-interneurons described by Westfall and associates (Westfall, 1966, 1970, 1973a, b, 1980; Westfall *et al.*, 1971; Westfall and Kinnamon, 1978; Kinnamon and Westfall, 1982), except that the cell apparently lacks a cilium. Tsuneki and Kobayashi (1977) describe two nerve cells in *Hydractinia epiconcha*, as had earlier workers with *Hydra* (*e.g.*, Lentz, 1966, 1968). The nerve cell in *H. echinata* resembles a combination of the traits described for the two cells of *H. epiconcha*.

The spatial distribution of the various cell types suggests a strong functional specialization of different regions along the surface of the planula. The competent planula is held in an upright posture with the blunt anterior end attached to sand grains and the tapered posterior end suspended above the sediment-water interface (pers. obs.). The anterior end is characterized by a distinct dimple, surrounded by numerous EMC's and mucous cells. The dimple, similar to that described for the *Cassiopeia xamachana* and *P. gurneyi* but lacking in many other free-swimming planulae, likely functions as a suction cup allowing sedentary planulae to temporarily adhere to stable substrata. The tapered end of the planula, which must first interact with approaching hermit crabs, is especially rich in neurosensory cells. These neurosensory cells are adjacent to high concentrations of nematocytes. The spatial association of neurosensory cells and nematocytes is particularly significant, given Spencer and Arkett's (1984) observation that patterns of intercellular electrical communication may be effectively localized by non-overlapping distribution of cell types. Nematocysts have been implicated in the process of securing the planula to the shell (Lyons, 1973; Muller, 1973; Chia and Bickell, 1978). These suggestions are given further support by the common laboratory observation that planulae will adhere to moving objects (Chia and Bickell, 1978; pers obs.). Surely the desmonemes with their thick, sticky thread might aid in contacting a shell, while isorhizas with their long barbed thread and stylet might aid in securing the initial attachment. Once on a shell, the planula must permanently attach and metamorphose. Martin and Thomas (1977) describe granules in EMC cells of *P. tiarella* similar to those found in *H. echinata* and note that these are absent in the adult, suggesting that apical granules are utilized in metamorphosis. The mucous cell of *Hydractina* are also concentrated at the blunt anterior end of the planula, where permanent adherance to a surface takes place. These cells possess a microvillar net, observed to control the release of mucous during metamorphosis by Crawford and Chia (1974), further implicating the mucous cell in attachment. The presence of dense staining granules of the EMC's in addition to mucous cells suggest the possibility of a "duo-gland adhesive system" as described by Hermans (1983).

While analysis of fine structure alone cannot insure accurate prediction of function, analysis of the fine structure and spatial distribution of ectodermal elements of the *H. echinata* planula suggest the following hypotheses regarding settlement: (1) the dimple of EMC's and mucous cells at the anterior end acts as a suction cup holding the planula upright on sand grains, (2) neurosensory cells sense the activities of nearby hermit crabs signaling a release of the suction, (3) the planula is drawn into contact with the crab by its feeding currents, initiating the discharge of nematocysts, and (4) the nematocysts adhere to the crab's shell facilitating the temporary attachment to the shell prior to eventual secretion by EMC's and/or mucous cells of substances used in permanent attachment.

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LITERATURE CITED

BALLARD, W. W. 1942. The mechanism of synchronous spawning in *Hydractinia* and *Pennaria*. *Biol. Bull.* **82:** 329–339.

BUNTING, M. 1894. The origins of sex-cells in *Hydractinia* and *Podocoryne*. *J. Morphol.* **9:** 203–236.

BUSS, L. W. 1979. Habitat selection, directional growth and spatial refuges: why colonial animals have more hiding places. Pp. 459–497 in *Biology and Systematics of Colonial Organisms*, G. Larwood and B. Rosen, eds. Academic Press, London.

CHAPMAN, G. B., AND L. G. TILNEY. 1959. Cytological studies of the nematocysts of *Hydra*. I. Desmonemes, isorhizas, cnidocils and supporting structures. *J. Biophy. Biochem. Cytol.* **5:** 69–78.

CHIA, F. S., AND B. CRAWFORD. 1977. Comparative fine structural studies of planulae and primary polyps of identical age of the sea pen *Ptilosarcus gurneyi*. *J. Morphol.* **151:** 131–158.

CHIA, F. S., AND L. BICKELL. 1978. Mechanisms of larval settlement and the induction of settlement and metamorphosis: a review. Pp. 1–12 in *Settlement and Metamorphosis of Marine Invertebrate Larvae*, F. S. Chia and M. E. Rice, eds. Elsevier, New York.

CHIA, F. S., AND R. KOSS. 1979. The structural studies of the nervous system and the apical organ in the planula larva of the sea anemone *Anthopleura elegantissima*. *J. Morphol.* **160:** 275–298.

CHIA, F. S., AND R. KOSS. 1983. On the fine structure of the nematocysts in the planula larva of a sea anemone, *Anthopleura elegantissima*. *Biol. Bull. Nat. Taiwan Normal Univ.* **18:** 11–24.

CRAWFORD, B. J., AND F. S. CHIA. 1974. Fine structure of the mucous cell in the sea pen, *Ptilosarcus gurneyi*, with special emphasis on the possible role of microfilaments in the control of mucus release. *Can. J. Zool.* **52:** 1427–1432.

HERMAN, C. O. 1983. The duo-gland adhesive system. *Oceanogr. Mar. Biol. Ann. Rev.* **21:** 283–339.

IVKER, F. B. 1972. A hierarchy of histocompatibility in *Hydractinia echinata*. *Biol. Bull.* **143:** 162–174.

JACKSON, J. B. C. 1977. Habitat area, colonization, and development of epibenthic community structure. Pp. 349–358 in *Biology of Benthic Organisms*, B. F. Keegan, P. O. Ceidigh, and P. J. S. Boadon, eds. Pergamon Press, New York.

KINNAMON, J. C., AND J. A. WESTFALL. 1982. Types of neurons and synaptic connections at hypostome—tentacle junctions in *Hydra*. *J. Morphol.* **173:** 119–128.

LENTZ, T. L. 1966. *The Cell Biology of Hydra*. Wiley, New York. 199 pp.

LENTZ, T. L. 1968. *Primitive Nervous Systems*. Yale University Press, New Haven, CT. 148 pp.

LYONS, K. M. 1973. Collar cells in planula and adult tentacle ectoderm of the solitary coral *Balanophyllia regia* (Anthozoa: Eusammiidae). *Z. Zellforsch.* **145:** 57–74.

MARISCAL, R. 1974a. Scanning electron microscopy of the sensory epithelia and nematocysts of corals and a corallimorpharian sea anemone. *Proc. Inter. Coral Reef Symp.* **2:** 519–532.

MARISCAL, R. 1974b. Nematocysts. Pp. 129–178 in *Coelenterate Biology: Reviews and Perspectives*, L. Muscatine and H. M. Lenhoff, eds. Academic Press, New York.

MARTIN, V. J., AND M. B. THOMAS. 1977. A fine structural study of embryonic and larval development in the gymnoblastic hydroid *Pennaria tiarella*. *Biol. Bull.* **153:** 198–218.

MARTIN, V. J., AND M. B. THOMAS. 1981a. Elimination of the interstitial cells in the planula larva of the marine hydrozoan *Pennaria tiarella*. *J. Exp. Zool.* **217:** 303–323.

MARTIN, V. J., AND M. B. THOMAS. 1981b. The origin of the nervous system in *Pennaria tiarella* as revealed by treatment with colchicine. *Biol. Bull.* **160:** 303–310.

MARTIN, V. J., AND M. B. THOMAS. 1983. Establishment and maintenance of morphological polarity in epithelial planulae. *Trans. Am. Microsc. Soc.* **102:** 18–24.

MARTIN, V. J., AND F. S. CHIA. 1982. Fine structure of a scyphozoan planula *Cassiopeia xamachana*. *Biol. Bull.* **163:** 320–328.

MARTIN, V. J., F. S. CHIA, AND R. KOSS. 1983. A fine structural study of metamorphosis of the hydrozoan *Mitrocomelia polydiademata*. *J. Morphol.* **176:** 261–287.

MEADOWS, P. S., AND J. I. CAMPBELL. 1972. Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.* **10:** 271–382.

MULLER, W. A. 1969. Auslosung der Metamorphose durch Bakterien bei den Larven von *Hydractinia echinata*. *Zool. Jb. Anat. Bd.* **86:** 84–94.

Muller, W. A. 1973. Induction of metamorphosis by bacteria and ions in the planulae of *Hydractinia echinata:* an approach to mode of action. *Publ. Seto Mar. Biol. Lab.* **20:** 195–208.

Otto, J. J. 1978. The settlement of *Haliclystus* planulae. Pp. 13–22 in *Settlement and Metamorphosis of Marine Invertebrate Larvae,* F. S. Chia and M. E. Rice, eds. Elsevier, New York.

Scheltema, R. S. 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavia* **10:** 263–296.

Slautterback, D. B., and D. W. Fawcett. 1959. The development of the cnidoblasts of *Hydra.* An electron microscope study of cell differentiation. *J. Biophys. Biochem. Cytol.* **5:** 441–452.

Spencer, A. N., and S. A. Arkett. 1984. Radial symmetry and the organization of central neurones in a hydrozoan jellyfish. *J. Exp. Biol.* **110:** 69–90.

Spindler, K. D., and W. A. Muller. 1972. Induction of metamorphosis by bacteria and by a lithium pulse in the larvae of *Hydractinia echinata* (Hydrozoa). *Wilhelm Roux Arch. Entwicklungsmech. Org.* **169:** 271–280.

Tsuneki, K., and H. Kobayashi. 1977. The fine structure of neurosecretory cells in the polymorphic hydroid *Hydractinia epiconcha. J. Fac. Univ. Tokyo (Sec. IV) Zool.* **14:** 35–46.

Vandermeulen, J. H. 1974. Studies of coral reefs. II. Fine structure of planktonic planula larva of *Pocillopora damicornis* with emphasis on the aboral epidermis. *Mar. Biol.* **27:** 239–249.

Westfall, J. A. 1966. The differentiation of nematocysts and associated structures in the Cnidaria. *Z. Zellforsch.* **75:** 381–403.

Westfall, J. A. 1970. Ultrastructure of synapses in a primitive coelenterate. *J. Ultrastruct. Res.* **32:** 237–246.

Westfall, J. A. 1973a. Ultrastructural evidence of a granule-containing sensory-motor-interneuron in *Hydra littoralis. J. Ultrastruct. Res.* **42:** 268–282.

Westfall, J. A. 1973b. Ultrastructural evidence for neuromuscular systems in coelenterates. *Am. Zool.* **13:** 237–246.

Westfall, J. A. 1980. Neuro-epitheliomuscular cell and neuro-neuronal gap junctions in *Hydra. J. Neurocytol.* **9:** 725–732.

Westfall, J. A., S. Yamataka, and P. D. Enos. 1971. Ultrastructural evidence of polarized synapses in the nerve net of *Hydra. J. Cell Biol.* **51:** 318–323.

Westfall, J. A., and J. C. Kinnamon. 1978. A second sensory-motor-interneuron with neurosecretory granules in *Hydra. J. Neurocytol.* **7:** 365–379.